

*Lystrus longimanus.*

*L. trapezoideus*, fusco-niger, parum nitidus; antennis ferrugineis; rostro dimidio basali lineis elevatis instructo; pedibus anticis valde elongatis, tibiis eorundem fortiter arcuatis. Long.  $2\frac{1}{2}$  lin.

*Hab.* Sumatra.

Trapezoidal, brownish black, slightly glossy, antennæ ferruginous; rostrum moderately long, basal half with raised lines, the intervals punctured; antennæ with the club as long as the funicle; prothorax rapidly broader to the base, with close-set granules in short transverse lines; scutellum round; elytra narrowly striate, the interstices broad, with contiguous punctures; body beneath densely covered with pale greyish scales; intermediate and posterior legs very short, ferruginous, the tibiæ of the former with a tooth on the outer edge at the base; fore legs very long, their tibiæ strongly curved, their tarsi of moderate length.

A broader species than *L. latipennis* (Linn. Soc. Journ. xii. p. 44, pl. iii. fig. 1) and differently sculptured. It is possible that the remarkably long anterior legs may be a sexual distinction, at least to a certain extent.

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L.—*On the Phylogeny and Anatomy of the Echinodermata.*

By Dr. OTTO HAMANN\*.

1. *Origin of the Echinodermata.*

If we set before us the question to what group of the Metazoa, with reference to the whole of their peculiarities of organization, are the Echinodermata most nearly related, the answer will serve at the same time to throw light upon their phylogenetic origin. I have said if we take into consideration "the whole of their peculiarities of organization," and therefore the constitution of the nervous system, the body-cavity, &c., and would thereby indicate that I must regard as failures all the attempts which look only to a single system of organs, such as has lately been made by Kleinenberg, who, by taking into consideration only the nervous system, has been led into the most wonderful speculations as to the origin

\* The concluding chapter of a memoir on the Histology of the Echinodermata, translated from the 'Jenaische Zeitschrift,' Band xxi. pp. 232-251.

of the Annelida from Medusæ, speculations and ideas which can hardly find confirmation in nature. The larval forms of the Echinodermata, the formation of the body-cavity, the enterocoel, the origin and structure of the nervous system, will chiefly point towards worm-like creatures, and indeed to *such forms as possess a typical enterocoel of like origin and development*, and in which the nervous system is either still situated in the ectoderm, as in the Asterida, or arranged in the same way as in the Echinida and Holothuriæ. To ascribe to the Echinodermata a near relationship to the Cœlenterata, as has been done by Kleinenberg, although certainly only in a remark *en passant* \*, will not do, for the agreement in the structure of the nervous system alone would not suffice to balance the great number of other differences of structure, as, for example, the existence of a body-cavity in the Echinodermata.

Among the groups of Vermes the Annelida, with their typical enterocoel, stand nearest to the Echinodermata, as Hæckel has long since shown; and, in fact, this notion is most particularly well supported, especially by the structure of the body-wall. In the Asterida there is in each arm a dermal muscular tube, consisting of a layer of annular and a layer of longitudinal muscles. In the Echinida the former exists only in a rudimentary form (Ludwig), while in the Holothuriæ it appears to be confined to definite zones.

As regards the structure of the nervous system, it is as simple as is conceivable in Asterida, consisting of epithelial sense-cells and nerve-fibres. But among the Vermes also, and, indeed, among the more highly developed of them, we find forms in which the whole nervous system persists throughout life in the ectoderm. This is the case in the Archannelida (Hatschek and Fraipont).

There is consequently no reason to prevent us from regarding the Echinodermata, although not as Annelida, yet as descending from Vermes provided with true body-cavities, in which the nervous system still remained in the lowest stage of development and in which a water-vascular system was probably already developed. But then the first question is, What group of Echinodermata is to be regarded as the earliest, and are the different divisions deducible from each other?

It is remarkable that the majority of zoologists and geologists regard the Crinoidea (or Cystidea) as those which have retained all organizational characters in their most primitive condition.

\* Zeitschr. für wiss. Zool. Bd. xliv.

Crinoidea and Asteroidea are of the same antiquity. Both groups make their appearance as early as in the Silurian formation. But the species which here first come under our notice are such as can by no means pass as primordial forms. These have not been preserved for us. This becomes intelligible if we consider that in them the calcareous skeleton, and therefore the parts best adapted for preservation, will have been still but scantily developed, and that in general all the remains of Asterida appear to be very badly preserved, so that they generally occur only in fragments. Hence we cannot expect that palæontology will ever elucidate the phyletic history of this group. This opinion, which has also been expressed by Zittel (*Handb. der Pal.* i. 1, p. 309), has not been adopted by other palæontologists, such as Neumayr\*, but they have established a genealogy of the Echinida almost exclusively upon palæontological data. Whether this genealogy is reconcilable with the anatomical data is a matter which I will briefly discuss.

According to Neumayr the Cystidea are to be regarded as the stock-group of the Echinodermata, therefore a group which others have united with the Crinoidea, and from them the Crinoidea are supposed to have branched off. This branching off is no further demonstrable, as both groups make their appearance side by side in the Lower Silurian, and earlier remains have not yet been found. The assumption that the Cystidea are the most ancient Echinid group has therefore not even a palæontological foundation. Further, according to Neumayr, the Ophiuroasterida have branched off from the Cystidea, and the Echinida in another direction. Other naturalists have already raised the question whether, if certain forms of Cystidea, such as *Agelacrinus*, remind us of the Asterida, this is not due to mere accidental external resemblances. The same applies no doubt to the resemblances which have been found between Cystidea (such as *Mesites*) and Echinida. As Hörnes says †, the genetic relations here are still very doubtful.

If we add to this that important objections have been raised against the homologization of the basal plates of the Crinoidal calyx with the apical plates of the Echinida (H. Carpenter), the probability of the derivation of the Echinida from the Crinoidea is still further diminished.

To all this must be added, and this gives the finishing

\* "Morphologische Studien über Echinodermen," in *Sitzungsb. d. k. Akad. Wiss. in Wien*, Bd. lxxxvi. (1881).

† 'Elemente der Paläontologie,' 1884, p. 173.

stroke, that anatomically and histologically it is impossible to accept the Crinoidea as the stock-group of the Echinodermata. Our present standpoint can only be that on the one side stand the Crinoidea and on the other the Asterida, from which the Echinida may be derived without any difficulty, and lastly the Holothuriæ. While the last-mentioned three groups can be derived, in their organization, from one another, the Crinoidea stand without any connexion.

Quite peculiar and present in no [other] group are the remarkable calycine pores, through which the body-cavity communicates with the outer world. Above all, however, the nervous system is not in the primitive form which occurs in the Asterida. This (the nervous ring and ambulacral nerve-stems radiating from it) is no longer situated epithelially, but subepithelially (Ludwig). The most important part of the nervous system of the Crinoidea is, however, placed dorsally, in the centro-dorsal plate; from a central organ fibrous cords are given off into each arm, and from these similar cords to the muscular fasciculi and appendages of the arms, as already described by W. B. Carpenter in 1865. A dorsal nervous system so constructed does not occur in the Asterida (Ophiuri), Echinida, or Holothuriæ.

We have also to consider above all the body-cavity of the Crinoidea, which is probably to be regarded as a schizocoelar cavity, and the sexual organs, the structure of which differs from that of those of the other groups.

I think, therefore, that the Crinoidea may be most naturally regarded as a lateral branch of the Echinodermata, about the origin of which we are still in doubt. As coming nearest to the truth we may perhaps suppose that the Crinoidea and the Asterida have sprung from a common root. I regard the latter as the stock-form of the most nearly allied Echinodermata, referring especially to the structure and ectodermal position of the nervous system. How I suppose the Echinida to have originated from them will be shown in the following pages.

Consequently I come to the conclusion that those naturalists, with Hæckel, G. O. Sars, and Lange at their head, who place the Asterida at the head of the Echinodermata, have hit upon the right course. Palæontology, it may be repeated, supports neither the one interpretation, according to which the Crinoidea are to be regarded as the most ancient class of the Echinodermata, most nearly approaching the stock-group (Claus), nor the other view, just maintained by me, as the two groups make their appearance together at the same time

in the Lower Silurian. The morphological data alone can be appealed to here for the decision of the question.

## 2. *The Relationship between Asterida and Echinida.*

Having described the organizational characters of the Echinida, I may attempt in what follows to bring together the reasons which give the greatest possible probability to the proposition that the Asterida must be regarded as the primordial group most nearly approaching the stock-form of the Echinodermata, and the Echinida to be derived from them, as has already been supposed by Hackel, Gegenbaur, and others.

I know very well that with many this assumption passes as an established proposition. For such what follows is written only to a limited extent, so far as they, unlike myself, are of opinion that this proposition is still unproven. I would also further show that it is only possible to explain the organizational characters of the Echinida if we derive them from those of the Asterida, and that this assumption alone admits of an unforced explanation of their structure.

Palæontology shows us that the Asterida are among the most ancient of organisms, and that there is nothing to prevent the Echinida, which are already represented in the Lower Silurian, being derived from them. Of course in this we have to consider only the regular Sea-urchins, but not the irregular ones, such as the Spatangidæ, which may with great certainty be regarded as later formations. Hence, when in what follows I speak of Echinida, it is especially only the regular Sea-urchins that I refer to.

In deriving the Echinid-organism from that of the Asterida, the *nervous system* must be taken into consideration in the first place. In the Starfishes the nervous system originates in the ectoblast\*, and retains its position in the ectoderm. This applies to the central nervous system, the cerebral ring, and five (or more) ambulacral nerve-trunks. The intestinal nervous system I leave on one side, as not essential in our comparison.

In the Echinida, when the animal is mature, the nervous system is no longer situated in the ectoderm; it has come to lie in the mesoderm; and in them we find it connected with the epithelium of the body only where sense-organs are present.

But are the elements which constitute the central nervous

\* See Ludwig, *Asterina gibbosa*.

system in the Echinida the same as those of the Asterida, or derivable from those of the latter group? To decide this question we may refer briefly to the constitution of the nervous system of the Asterida. The cerebral ring and the ambulacral nerves consist of nerve-fibres intermixed with ganglion-cells, which run between the processes of the unusually elongated, filiform, epithelial cells of the ambulacral groove. These epithelial cells I have named "supporting-cells," and their basal processes "supporting-fibres;" the latter are the so-called transverse fibres of older writers, which run perpendicular to the nerve-fibres. In the Echinida the central nervous system consists of the following elements:—the nerve-fibres with the ganglion-cells, and, applied to these, cells the nature of which may be a matter of dispute. This coating of cells, which lies peripherally upon the main nerve-stems and the central ring, is regarded by Frédéricq as nervous—it is supposed that we have here to do with ganglion-cells which lie upon the cords of nerve-fibres in the same way as is the case in many Vermes, for example.

Whether these cells have acquired the function of ganglion-cells seems doubtful to me. Judging from their origin *they are epithelial cells which have come to lie in the mesoderm together with the nerve-fibres originally (in the ectoblast) epithelially situated and produced.* In the first place they function as a covering epithelium, a protective coat for the fine nerve-fibres, as I have already shown in the Holothuriæ, and as seems to me to follow pretty certainly from a comparison with the Asterida.

That these cells form a covering epithelium, a protective covering, appears further from *their basal supporting-fibres, which traverse the nerve-fibres perpendicularly.* These supporting-fibres have, however, hitherto escaped the notice of naturalists in the Echinida. I believe that even those who are inclined to interpret the covering-epithelium as of nervous nature can no longer, after the discovery of the supporting-fibres, uphold this opinion to its full extent. But what further goes against the nervous nature of these cells is their difference in form and size from the true nerve-cells in the main trunks, and the nerve-cells which form a peripheral coating at the point of bifurcation of the main nerve-cords.

The ganglion-cells which are situated in the main trunks and the cerebral ring possess an oval nucleus, which always stains of a lighter colour than the nucleus of the covering-cells. A nucleolus is usually to be seen. The size of the ganglion-cells is different from that of the covering-cells.

The latter are always smaller and generally possess a basal cell-process, a direct continuation of the cell-substance, which shows a different refractive power from the nerve-fibres, and therefore, if only on that account, has nothing to do with them, and, further, is much stronger and has a greater diameter.

The ganglion-cells, as they occur in the peripheral parts of the nervous system, are of two different forms. If they lie within the nerve-fibres, the nerves of the skin (I am referring to nerve-cords), they have the same form as in the main trunks. Besides this kind cells occur which are characterized by their size, their large pale nuclei, and their constantly distinct nucleoli. These lie peripherally upon the nerve-cords, and where nerve-fibres issue from the nerve-cords, for example to run to the muscular fibres (in the pedicellariæ the ramifications between the musc. adductores, in the basal annular nerve of the spines of *Sphærechinus*, *Echinus*, *Centrostephanus*, &c.), form a coating between the muscular fibres embraced by the nerve-fibres. These cells measure about 0·07 millim., and their circular nuclei 0·002–0·003 millim. That they differ widely from the cells of the covering-epithelium there can be no doubt.

If I have discussed the question of the interpretation of these coating-cells in a detail which may appear superfluous to many, this is due to the wish to render my description as conclusive as possible.

If we are to derive the Echinida directly from the Starfishes, we must seek in them for organs homologous with *the tentacle and eye-spots*. As is well known there are upon the intergenital plates (ocellar plates) in many Sea-urchins pigment-spots which it has been supposed might be interpreted as eyes, seeing that they are situated in spots homologous with the ends of the arms of Starfish. As I have already shown, we have to do here by no means with structures resembling the eye-spots of Starfishes, but only with accumulations of pigment which may sometimes be present, sometimes absent. But that we may in this case with some justice speak of degenerations of the eye-spots appears from the presence of a tentacle, although a modified one, in the Echinida\*. The tentacle pierces the intergenital plate, and thus comes to lie partly in and partly upon the latter. A water-vessel (ambulacral) and a nerve-trunk terminate in it in the same way as in the Starfishes. Nay, even mobility cannot be wholly denied to the Echinidan tentacle, seeing that it, or

\* See Hamann, "Vorl. Mitth. zur Morphol. der Echiniden, No. 5," in Sitzungsab. der med.-naturw. Gesellschaft zu Jena, 1886, Heft 2.

at least its terminal portion which rests upon the plate, can very well be inflated by the water-vessel which terminates cæcally in it, and in this way may be pushed forth, though only to a limited extent. Perhaps Sea-urchins still exist in which there are eye-spots like those of the Starfishes, and in which the resemblance of the tentacles of the two groups will be still greater. This, however, appears to be doubtful, inasmuch as, where true organs of vision are at present known in Sea-urchins, these have been found upon the surface of the test, where, especially when present in great number, they must be of essential service to the animals\*.

Of equal importance for the question of the derivation of the Echinida from the Asterida is a *comparison of their sanguiferous spaces*, i. e. *the whole of the schizocœle structures*.

In the Starfishes there is in the body-wall a system of lacunæ and hollow spaces, which have been in part described as perihæmal spaces (Ludwig). All these lacunæ and spaces are gaps in the connective substance, schizocœle-spaces, as I have demonstrated in opposition to the previous supposition that they are parts of the enterocœle, by tracing their origin. In the ventral wall such a schizocœle-space runs into each arm. We find them again in the Sea-urchins in each ambulacrum, and here likewise terminating cæcally, in this case by the intergenital plate, in the former (Starfishes) by the tentacle. But while in the Starfishes these five spaces or canals unite in the centre to form an annular canal, which is connected through the tubular canal with the schizocœle-spaces in the dorsal body-wall, the conditions are different in the Echinida, seeing that in them a masticatory apparatus has been developed (probably from vertical plates), and the tubular canal occurs only as a rudiment. Moreover, in the Sea-urchins there is retained only a remnant of the schizocœle-system of the dorsal wall of the Starfishes, in the form of the *schizocœlar anal ring*, as I have already shown †, from which structures lead to the sexual organs, like those presented by the Starfishes. That all these phenomena may be easily explained by the origination of the Sea-urchin from the Starfish is perfectly clear, while the reverse mode of origin seems almost inconceivable, or, at any rate, is less probable.

In the five schizocœle-spaces (longitudinal canals) of the ventral wall ("perihæmal spaces" of Ludwig) of the Asterida connective partitions (septa) have, as is well known, been developed, and in these formation of unwallled spaces (the blood-lacunæ) has taken place.

\* See Sarasin's statements, Zool. Anz. 1885.

† See also my "Vorläufige Mittheilungen," already quoted.



That we find the ventral longitudinal canals of the Asterida again in the Echinida I have already shown.

But what we do not find in the Echinida (and Spatangida) are the septa, the longitudinal partitions of the ventral longitudinal canals with hollow spaces developed in them, the true blood-lacunæ. This may be explained in the following way: In the Asterida, as the more ancient forms, the central nervous system remains throughout life in the ectoderm, where it originated, while in the Echinida at a certain time it separates from the ectoderm and moves into the longitudinal canals. In the Sea-urchins the longitudinal canals (*i. e.* the canals indicated as perihæmal spaces in the Starfishes) are traversed throughout their whole extent by the five ambulacral or radial nerve-trunks. By this means of course a development of partitions or septa is rendered impossible. If we speak of perihæmal canals in the Starfishes, in the Sea-urchins we must call them perineural canals.

These perineural canals have no connexion at all with the system of blood-lacunæ. The lacunar ring, which in the Starfishes runs round the œsophagus, has in the Echinida come to be situated upon the lantern, and from it start the lacunæ to the intestine and the glands.

In schizocœle-formations of the back the blood-lacunæ run, in the same way as in the Asterida, in septiform structures. Moreover the Asterida and Echinida exhibit similar structures in the blood-lacunæ running to the sexual organs.

In Starfishes a schizocœle-space runs to each sexual organ and is continued in lacunæ of the connective substance of the wall of the organ. But in each schizocœle-space there runs also in the suspensory band a blood-vessel (according to Ludwig's designation), which is connected with the glandular organ. I regard these canaliculi also as conductive lacunæ for the glandular organ. The cells in them will certainly have taken up materials from the sexual organs to be conveyed towards the glandular organ. That excretory materials are found in the lacunæ of the wall of the sexual organ may be easily proved by sections. Deposits of granules, sometimes of a brownish, sometimes of a yellow colour, occur everywhere. Nay, it has even been said by one naturalist that the sexual organs, at the time when they do not form ova or semen, function as glands!

In the Echinida the anatomical character is the same. In them also schizocœle-spaces pass to the organs and enclose the peculiar lacunæ situated in the walls. The foundation of the sexual organs is the same in both groups. Nay, the figures which show the sexual organ in the Echinida still in

the form of an oval vesicle projecting into a vacant space (schizocoele-space) might equally well be drawn from a Starfish.

In Asterida a follicular epithelium could be demonstrated. In Echinida the first foundation of the ovicell from epithelial cells is so far the same that here also a commencement of follicle-formation is made. It goes no further, however, and the developed Echinidan ovum possesses a resistant envelope, which, however, has been formed from the ovicell and not from a follicular epithelium.

An apparently great difference in the organism of the Seaurchin is constituted by the presence of a special masticatory apparatus, the lantern. That this is produced by alteration and transformation from whorls of the Starfish seems to be probable. But that no Starfish can be produced from a Seaurchin provided with a masticatory apparatus is shown with certainty, in my opinion, by the position of the oral blood-lacunar ring and of the water-vascular annular canal. The peculiar positions of these organs in Echinida are in relation to their simpler and more easily intelligible position in the Starfish under the condition of the changed position of the whorls.

A further important agreement is shown by the *water-vascular system*. The stone-canal of the Asterida is of very complex structure and forms a smooth-walled tube only in youth. Later on spiral convolutions of various forms appear in the lumen. In the Echinida the canal remains a smooth tube and shows no organization indicative of the structures occurring in Starfishes. This retrogression, as I conceive the simplicity of this organ in the Echinida to be, is closely connected with the mode of life of these animals. Their movement is in most cases limited in extent. The sucking-feet are only moderately effective, owing to the long spines, and locomotion takes place usually with the aid of the spines employed as stilts. Through this a retrogression of the longitudinal canals (ambulacral vessels) of the aquiferous vessels has taken place; the ampullæ are less developed, and the valves occurring in Asterida have disappeared. In their place the transversely-stretched muscular threads provide for the closure of the ampullæ, but of course only in a very insufficient manner. Most of the ambulacral feet are therefore but little developed, and this applies particularly and in a still greater degree to the Spatangidæ, in which the retrogression has gone much further.

In two or three words I must refer to the disappearance of the musculature of the body-wall in the Echinida. In the

Starfishes I have demonstrated in the body-wall of each arm an annular and a longitudinal muscular layer, such as exist in the same way in the Vermes. In the Echinida the rays (the arms) are amalgamated with the body, the calcareous secretions form a skeleton consisting of ten pairs of plates, for which muscles in the body-wall have become unnecessary. If, then, we assume that the Holothuriæ have branched off from the Echinida, this must have occurred early, that is to say they must have originated from forms in which the musculature had not yet retrograded nor the skeleton been developed, as is the case in existing Echinida. According to Ludwig's \* discovery in Spatangidæ, on the dorsal surface between the rows of plates situated above the periproct there are muscular fibres at the point where they meet in the middle line. This musculature, which consists of short (1 millim. long), smooth, muscular fibres, notched at their extremities, is to be regarded as the remnant of the annular (and longitudinal) musculature of the body-wall, such as is shown by the Starfishes.

### 3. *What Structures are we to regard as Sanguiferous Spaces in the Echinodermata?*

The older naturalists supposed that in the Asterida the five or more longitudinal canals running in the ventral surface of the arms were the blood-vessels, and that the annular cavity surrounding the œsophagus, which unites these five or more canals, was the annular vessel. It was shown, however, by Lange and Teusch, that these radial or ambulacral longitudinal canals were divided in their whole length by a vertical band, and that this band in its whole extent was traversed by interstices and cavities. In the latter they recognized the true blood-vessels, or rather blood-lacunæ. That the conditions are the same in the dorsal body-wall, and that here also the true blood-lacunæ (the anal ring of blood-lacunæ and the lacunæ leading to the sexual organs) lie in such canals, has been shown by Ludwig, who proposes the name of *perihæmal canals* for the latter. At the same time, however, that naturalist supposed that the perihæmal canals were in connexion with the body-cavity, the enterocœle. I have shown, by demonstrating the origin of these canals as also of the ventral blood-lacunæ, that perihæmal cavities as well as blood-lacunæ of the septa or suspensory bands are schizocœle-formations and therefore homologous structures. This applies also to the cavitory system dis-

\* "Ueber bewegliche Schalenplatten bei Echinoideen," in Zeitschr. für wiss. Zool. Bd. xxix.

covered by Greeff in the connective substance of the cutis of the dorsal wall. These cavities are connected with the perihæmal spaces and the so-called tubular canal.

Taking all this into consideration we have in the Asterida a series of schizocœle-structures to which the five or more ventral radial canals (perihæmal spaces) belong, and, further, the blood-lacunæ running through septa, likewise schizocœle-cavities.

What do we find of these two systems of cavities in the Echinida?

In the regular Echinida we find the five longitudinal canals, in which the five ambulacral or radial nerve-trunks have come to lie. Further, we find a cavity enveloping the annular nerve at one of its surfaces, a homologue of the annular perihæmal cavity in the Asterida. Besides these we have to note an anal annular schizocœle-cavity, with cavities which run to the sexual organs. These are the sole remains of the great dorsal canal-system of the Asterida; in their wall, *i. e.* in the wall of the anal schizocœle-cavity and partly projecting into it, lies the anal ring of blood-lacunæ, and, in the cavities running to the sexual organs, the blood-lacunæ. Consequently in the dorsal part of the Echinida the same conditions exist as in the Asterida. Here also we may speak of perihæmal cavities. The different character of the ventral surface is to be explained by the formation of the masticatory apparatus and by displacement of the five radial nerve-trunks, which have deserted their epithelial position and moved into the schizocœle-cavities. The septa with the blood-lacunæ (in the longitudinal canals), and therefore the true radial blood-lacunæ of the Asterida, have disappeared. But, on the other hand, a pericæsophageal ring of blood-lacunæ has become developed upon the lantern, and from this the blood-lacunæ run, as in the Asterida, to the gland, intestine, &c.

In the Spatangida, which are quite certainly to be derived from the Echinida, these conditions are as follows:—The masticatory apparatus has disappeared, and with it the pericæsophageal ring of blood-lacunæ situated upon it. In the five longitudinal canals (perihæmal canals) which open into an annular canal situated around the cæsophagus lie the (radial) ambulacral nerve-trunks and the circumoral nerve-ring as in the regular forms. But the blood-lacunæ (dorsal and ventral) of the cæsophagus open into this annular schizocœle-canal. This, consequently, in the Spatangidæ is to be regarded as a blood-lacunar ring, and the five longitudinal canals given off from it as the five ambulacral blood-lacunæ.

Thus in the Spatangida there has occurred a fusion of the cavitory systems, which in the Asterida are separate. In the dorsal part the blood-lacunæ run in the wall of the schizocœle-sinus, as I have shown for the first time. In this, therefore, these forms agree with the regular Echinida and the Asterida.

Let us now consider the Holothuriæ. In *Synapta* there is a blood-lacunar ring of very feeble construction running in the wall of the annular water-vascular canal. From this blood-lacunæ issue to the tentacular canals. In this genus no schizocœle-cavity runs through the five ambulacra. In the foot-bearing Holothuriæ, which show more primitive conditions, however, we again find the five radial ambulacral schizocœle-cavities; here they may justly be denominated blood-lacunæ.

In the Crinoidea we find radial longitudinal canals, which, as I propose to demonstrate immediately, are likewise schizocœle-structures, and are, certainly with justice, described as the radial blood-vessels by Ludwig. Greeff and Ludwig declared them to be homologous with the radial longitudinal canals (perihæmal cavities of Ludwig) in the Asterida. Subsequently Ludwig has retracted this opinion, because he thinks that the longitudinal canals of the Asterida are not themselves blood-lacunæ, but that the latter are situated in the septa, so that the blood-lacunæ of the Asterida and Crinoidea are quite different structures. The foundation of this opinion is to be found in the fact that Ludwig regarded the longitudinal canals as enterocœle-structures. When Ludwig further says that in the Crinoidea no perihæmal cavities have yet come into development, either in the periphery of the oral blood-vascular ring or in that of the radial blood-vessels, we may reply as follows:—The radial blood-vessels (so-called) of the Crinoidea and their oral blood-vascular ring are nothing but the radial longitudinal canals (perihæmal cavities) of the Asterida and their oral annular canal. But while in the Asterida special lacunæ, the true blood-lacunæ, have been developed in septa, the septa are wanting in the Crinoidea. The blood moves in the longitudinal canals, as is partially the case in Spatangida and Holothuriæ.

Further, the Crinoidea also possess other radial schizocœle-canals (homologous with the dorsal cavities of the other Echinodermata), and in these (in septa) blood-lacunæ occur, as will hereafter be shown in detail.

Summing up briefly all these conditions, it appears that no decided difference exists between true blood-lacunæ, situated

in septa which are extended in the radial schizocœle-cavities and the latter themselves; both structures are schizocœle-structures, and originate as spaces and cavities in the connective substance. To this must be added that the young *Asterias* of perhaps a centimetre in diameter has no cavities in its septa of the ventral surface, but that in this case the longitudinal canals (perihæmal cavities) must rather function as sanguiferous spaces. In future, when we speak of the blood-lacunar system in the Echinodermata it will no longer do to characterize as blood-vessels one set of structures in one group and another in another, but it will have to be shown how sometimes one and sometimes another part of the schizocœle-structures conveys the true blood-fluid and stands connected with the intestinal lacunæ.

We have therefore before us two different schizocœle-structures, two contrary systems, at first (*Asterida*) separated from one another, but which may afterwards partially communicate. The following table gives a summary representation of these schizocœle-structures:—

ASTERIDA possess:—	<i>Five or more radial (ambulacral) longitudinal canals (so-called perihæmal canals) in the ventral wall of the arms and an oral annular canal.</i>	<i>Blood-lacunæ situated in the septa of the longitudinal canals and an oral blood-lacunar ring.</i>	<i>Blood-lacunæ at the vertical pole in septa of the dorsal schizocœle-cavities.</i>
ECHINIDA.	Present (as neural canals).	Wanting; pericesophageal lacunar ring upon the lantern, with no connexion with the longitudinal canals. Intestinal lacunæ opening into it.	Present.
SPATANGIDA.	Present; the oral annular canal has become connected with the intestinal lacunæ!	Wanting; blood-lacunar ring deficient.	Present.
CRINOIDEA.	Present; the oral annular canal connected with the intestinal lacunæ.	Wanting.	Present (situated partly in the arms).
HOLO- THURIAE p.	Present; the oral annular canal connected with the intestinal lacunæ.	Wanting.	Wanting.

#### 4. Summary of Results, with a Description of the Principal Conditions of the Anatomical Structure of the Sea-urchins.

In giving the following description of the anatomical and histological structure of a Sea-urchin, I indicate only the principal results which seem to me to be of importance for the comprehension of the Sea-urchin's body. At the same time I do not refer at all to the skeletal characters, seeing that these are already sufficiently known and investigated, especially through the works of Lovén and other naturalists.

In the Holothuriæ, which are destitute of any spines or similar structures, I have been able to describe the sense-organs situated in the skin. In the Sea-urchins these are nearly all (with the exception of the tentacles) placed upon stalked organs, the pedicellariæ. By this means an efficiency is secured to them which sense-organs on the skin could not develop on account of the frequently very long spines.

On the pedicellariæ, with their three-valved forceps, the mechanism of which I have described in detail, supposed sense-organs were observed by Sladen only in one form, the so-called gemmiform pedicellariæ; but neither that naturalist nor Köhler succeeded in demonstrating nerve-terminations.

Exquisite sense-organs occur in all pedicellariæ—gemmiform, tridactyle, and trifoliate. Special tactile eminences, often of complex structure, occur on the inner surface of the valves; these are beset with rigid setæ. Nerve-branches run to these tactile eminences. In general three nerve-cords, composed of the finest nerve-fibres and ganglion-cells, were observed; these pass into the capitular part, and while each gives off numerous lateral branches to the musculature, sense-epithelium, &c., they could be traced to the tip of each valve. The glandular sacs in the wall of the pedicellariæ are of particular importance in the seizing of any objects; whether they exert a paralyzing action upon smaller animals, such as worms, is still to be ascertained.

Following on these organs come the *globiferi*, newly discovered organs which serve as weapons. They occur only in a few genera. As further appendicular organs of the skin Lovén's remarkable *sphæridia* are to be mentioned. At their base may be found a nerve-ring of the same structure as that which is detected on the spines. From this basal nerve-ring, which shows itself externally by a thickened epithelium, an epithelial pad, nerve-fibres run sometimes to the musculature, sometimes running to the apex of the spine in the four, five, or more long ciliary bands. Similar nerve-structures occur

between the *sutural lines* or *semites* of the Spatangida; only in these the nerve-fibre layer, which is epithelial in position, is more strongly developed generally in the whole of the dorsal epithelium, but especially in that of these sutural lines.

Nerve-terminations are observed in the *ambulacral feet*, especially in the peculiar pencil-like foot of the Spatangida. The complex structure which occurs in the sucking-plate of the foot of a regular Sea-urchin can only be described by reference to the figures.

In the *epithelium*, the *epidermis*, which covers all the external organs, nerve-fibres occur everywhere. They are all epithelial in position, or only partially so; in the latter case they run subepithelially in the layer of connective substance, the cutis. The body-wall of a Sea-urchin is composed, as is well known, of the outer epithelium and the cutis with the calcareous plates or separate calcareous bodies, as, for example, in the buccal disk, or also at the vertical pole (in *Centrostephanus longispinus*). In the body-wall, and indeed in the middle of the paired, so-called ambulacral plates, run five *longitudinal canals*. They commence at the vertical pole beneath the five intergenital (ocellar) plates, and run to the lantern, the masticatory apparatus. They are schizocœle-structures, longitudinal canals, in the connective layer. Into them have been shifted the five ambulacral (or radial) nerve-trunks, which in the Starfishes are still situated in the ectoderm. These nerve-trunks terminate on the one hand in the intergenital plates, on the other they pass into the lantern and form a nerve-ring which, on one side, is enveloped by a continuation of the longitudinal canals. In and upon the intergenital plates there is a rudimentary tentacle without any visual spots. The nerve-trunks consist of very fine nerve-fibres and ganglion-cells and of a cellular coat which is in part composed of supporting cells. This epithelium is to be regarded as homologous with the epithelium of the ambulacral grooves of the Asterida, not only the nervous mass itself, but the whole epithelium, having come to be situated in the mesoderm, as in the Holothuriæ.

From the nerve- or central ring nerve-cords are given off to the œsophagus, and these may be traced throughout the whole course of the intestinal tract. Parallel to the ambulacral nerve-trunks run the five *ambulacral water-vessels*; they terminate cœcally in the intergenital plates, while at the masticatory apparatus they ascend upon its outer surface and enter into the water-vascular ring, which lies upon the surface of the masticatory apparatus (the lantern) and surrounds the œsophagus. From this water-vascular ring the



stone-canal takes its origin, ascends perpendicularly upwards, and opens outwards through the pores of madreporic plates. The latter possess no arrangement by which they can be closed; they are rather always open for the entrance and exit of the sea-water on the one hand, and of the fluid contents of the water-vascular system on the other.

The *sanguiferous cavities* consist of the following parts:— In the first place the five longitudinal canals and the annular space enveloping the nerve-ring. In the Echinida these structures have nothing to do with the true blood-lacunæ; the latter originate as ventral and dorsal intestinal lacunæ from the blood-lacunar ring which lies upon the surface of the lantern. From the dorsal intestinal lacuna branches ramify which run to the glandular organ (the so-called heart of previous writers) and surround it. At its terminal portion (it extends into the body-wall and, indeed, into the schizocœle-sinus of the anal pole) lacunæ of the anal blood-lacunar ring are in connexion with this organ. This lacunar ring runs in an annular schizocœle-sinus surrounding the anus, partly projecting into it, partly in its wall; from it blood-lacunæ are given off to the sexual organs.

Peculiar organs are the five vesiculiform lobate structures situated upon the surface of the lantern, and previously described as *Polian vesicles*. From the water-vascular ring a canal leads into them, opening into their cavity, while blood moves in the connective wall in lacunæ which stand in direct communication with the blood-lacunar ring.

In the Spatangida there are present the five longitudinal canals and the œsophageal sinus communicating with them. The true blood-lacunar ring has, however, disappeared with the lantern, and both the dorsal and ventral intestinal lacunæ open into this œsophageal sinus, in which the nerve-ring is situated, and which has been designated the blood-lacunar ring. The dorsal lacuna, however, runs beside an intestinal water-vessel, which latter originates from the annular canal, which likewise concentrically surrounds the buccal aperture. This water-vessel and the intestinal lacuna communicate with each other in their further course, and run along the gland until the true stone-canal, originating from the madreporic plate, enters into the web of vessels produced by the amalgamation.

In this way is produced a communication between the water-vascular system and the blood-lacunar system, and thus between cavities of entodermal and schizocœlar origin, such as occurs in no other group of Echinodermata. That this

condition is secondary may be asserted most decidedly, as the Spatangida are palæontologically the youngest forms.

A remarkable organ is the "ovoid gland," the structure formerly designated the heart. So far as one is justified in judging from the extant results, we may regard it as an organ in which materials no longer available for the body are deposited. Blood-lacunæ open at the ends into it or surround it, as in the Echinida. No efferent duct has yet been found in any group.

The origin of the sexual products is of especial interest; they consist of primordial germ-cells (*Urkeimzellen*), as I have proposed to name these cells. They lie in the dorsal wall in an annular genital tube, on which five sacciform diverticula are formed, into which the primordial germ-cells pass. These diverticula form the first foundations of the sexual tubes. From the primordial germ-cells the ovicells are produced by growth &c.; and by division &c. the sperm-cells, as well as the whole of the epithelium which afterwards lines the sexual organs.

In mature animals these sexual tubes are atrophied. How far a similar origin of the sexual products from such primordial germ-cells prevails in all Echinodermata I shall show immediately in another place (*Zeitschr. für wiss. Zool.* Bd. xlvi. Heft 1).

LI.—*On the Mammals collected by Captain C. E. Yate, C.S.I., of the Afghan Boundary Commission.* By J. SCULLY\*.

MR. WOOD-MASON has asked me to contribute a paper on the collection of mammals and birds made by Captain C. E. Yate in Northern Afghanistan, and presented by that officer to the Indian Museum; the following notes are the result. The collection, I understand, was made after the departure of the naturalist of the Commission, so it may possibly include some forms not secured by him, and doubtless additional localities will now be made known for many of the species previously obtained.

\* From a separate impression from the 'Journal of the Asiatic Society of Bengal, part ii. 1887, communicated by the Author. [The section relating to the Birds has not been reprinted, as it consists, almost exclusively, of a list of the species observed.]